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4×–2× Potato Clones with Resistance or Susceptibility to Internal Heat Necrosis Differ in Tuber Mineral Status

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ABSTRACT

Internal heat necrosis (IHN) is a physiological disorder resulting in necrotic tissue in the pith of potato (*Solanum* spp.) tubers. Susceptibility is associated with localized Ca deficiency within the tuber, but Ca availability may be influenced by other nutrients. Studies in Virginia, North Carolina, and New Jersey in 2001 and 2002 determined the influence of soil-applied Ca on tuber yield, specific gravity (SG), IHN, and nutrient concentration. Furrow-applied Ca sulfate (448 kg ha^{-1} Ca) was applied to IHN resistant or susceptible interspecific 4×–2× *S. tuberosum* L. (*tbr*) × *S. phureja* Juz. & Bukasov–*S. stenotomum* Juz. & Bukasov hybrids. Tuber yield, SG, incidence and severity of IHN, and pith concentrations of P, K, Mg, Ca, S, Na, Zn, Mn, Cu, and Fe were determined. Clones differed significantly for yield, SG, and IHN expression. Resistant clones were lower in IHN incidence than susceptible clones, but the clone × Ca interaction was not consistently significant within location–years. Incidence was fit with a classification and regression tree (CART) model with the 10 nutrients as regressors, which revealed that IHN-resistant clones had higher tuber concentrations of Mn and S, but lower P. These results suggest that resistance or susceptibility to IHN is a complex function of tuber tissue mineral status. Mn, S, and P may make a more important contribution to clonal IHN resistance than Ca. Additional work is needed to verify the potential for minimizing IHN by either nutrient management or genetic enhancement.

INTERNAL HEAT NECROSIS, also known as internal brown spot (IBS), is a physiological disorder that is characterized by necrotic tissue appearing in the pith of potato tubers, usually toward the apical end of the tuber parenchyma. Growers in the mid-Atlantic region experience recurring quality problems due to the expression of IHN. Informal surveys of growers and Cooperative Extension agents indicated that in 2004, 10 to 15, 12, and 2% of the potato acreage in North Carolina, Virginia, and New Jersey, respectively, was lost to internal disorders. Sterrett et al. (1991b) found that the expression of IHN was influenced by temperature stress early in the growing season, the number of rain events, and growing conditions as reflected in tuber size distribution. Since the expression of IHN varies from year to year, screening for IHN resistance requires multiple location–years.

Efforts to breed IHN-resistant cultivars with high SG have been hampered by the narrow genetic base within *tbr* (Mendoza and Haynes, 1974). B5141–6, originally released as 'Lenape' (Akeley et al., 1968), and subsequently withdrawn for high glycoalkaloids (Anon., 1970), is the primary genetic source of high SG among U.S. potato cultivars (Douches et al., 1996; Haynes et al., 1995). The two major potato chipping cultivars currently grown in the mid-Atlantic region are 'Atlantic' and 'Snowden'; both are progeny of B5141–6 (Love, 1993). They are also both susceptible to IHN. Henninger et al. (2000) reported no relationship between SG and susceptibility to IHN within the USDA/ARS *tbr* breeding population; however, clones derived from Atlantic were more susceptible to IHN. Development of high SG, IHN resistant clones utilizing *tbr* alone have so far been unsuccessful. A diploid hybrid potato population of *S. phureja–S. stenotomum* has been extensively improved for high SG (Haynes et al., 1995; Haynes, 2001). High SG clones from this population have been utilized in 4×–2× crosses with *tbr* as the tetraploid parent. Sterrett et al. (2003) identified clones with significantly less IHN than Atlantic among the progeny of these crosses. The physiological and/or biochemical mechanisms governing IHN resistance in this germplasm is unknown.

The relationship between tuber Ca concentration and susceptibility to IHN is unclear. Kratzke and Palta (1986) used a divided-pot system to investigate Ca uptake from tubers and basal roots. They concluded that Ca concentration in tuber peel and pith tissue could be increased by the addition of Ca to the tuber and stolon region but not through basal roots. Application of Ca in a preplant strip increased Ca uptake in periderm and pith tissue compared with sidedress or broadcast treatments (Palta, 1996; Simmons et al., 1988). Tzeng et al. (1986) reported that tuber Ca concentration was negatively correlated with incidence of IBS in 'Russet Burbank' (*tbr*) on sandy soils that were low or deficient in Ca. Atlantic has significantly less pith tuber Ca and a significantly greater percentage of tubers with IHN than the IHN-resistant 'Superior' (Sterrett and Henninger, 1991). Sterrett and Henninger (1991) found that $CaSO_4$ banded in the seedpiece furrow significantly reduced the percentage of tubers with IHN and the severity of IHN in Atlantic, but IHN was not sufficiently reduced to meet U.S. No. 1 grading standards of no more than 5% internal defects by weight (USDA, 1972). Similarly, Silva et al. (1991) reported that reduction in incidence of

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Abbreviations: CART, classification and regression tree; IBS, internal brown spot; IHN, internal heat necrosis; *tbr*, *S. tuberosum*; SG, specific gravity.

IBS with applications of 560 or 840 kg ha^{-1} gypsum were partial and inconsistent. Kleinhenz et al. (1999) noted a reduction in internal defects (including hollow heart) in Atlantic from 16.4 to 10.6% with tuber pith tissue Ca exceeding 100 μg g^{-1}. However, Davies (1998) reported that there is no clear threshold value for Ca below which IHN is expressed. He reported that the correlations of Mg and phosphate with incidence of IHN were higher than for Ca, whereas the correlations of Na, K, B, Al, Mn, Fe, Co, Cu, Zn, Sr, Mo, and Ba with incidence of IHN were poor.

Research by Bamberg et al. (1993) has suggested that there are species differences in the ability to accumulate Ca in the tubers. They evaluated unpeeled tuber Ca accumulation ability among 21 *Solanum* species. In a low (80 ppm from tap water) Ca environment, *S. stenotomum* accumulated 187% more Ca than *tbr*. Unfortunately, they did not evaluate *S. phureja*. The potential for improved tuber Ca concentrations from *S. stenotomum* and the identification of both susceptible and resistant 4×–2× hybrids provides the opportunity to examine the relationship between susceptibility to IHN and the ability to accumulate Ca or other nutrients in tuber tissue.

Davies (1998) suggested that the nutritional status of the tuber with respect to IHN-resistance should be more thoroughly investigated. The purposes of this study were to (i) investigate the influence of Ca applied to Ca-sufficient native soils on yield, SG, expression of IHN, and nutrient composition of genetic material with known resistance or susceptibility to IHN; and (ii) determine the relationship among nutrient concentrations within the tuber pith and susceptibility or resistance to IHN.

MATERIALS AND METHODS

Controlled crosses were made during the spring of 1991–1993 between advanced tetraploid *tbr* clones or cultivars and diploid *Solanum phureja–S. stenotomum* clones. The resulting 4×–2× clones were screened for susceptibility to IHN in 1999 and 2000 in Plymouth, NC, Painter, VA, and Bridgeton, NJ (Sterrett et al., 2003). On the basis of those evaluations, nine of the most IHN-susceptible and eight IHN-resistant clones were chosen for this study. Atlantic was included as the susceptible standard.

At each mid-Atlantic location, the factorial study (18 clones × 2 $CaSO_4$ rates) was planted in a randomized complete block design with three replicates. $CaSO_4$ (0 or 448 kg ha^{-1} Ca) was applied as an in-furrow treatment over the seedpieces before covering. Each plot consisted of 20 hills spaced 0.23 m within the row at each location. Clones were planted in a different site each year on a Portsmouth fine sandy loam soil (fine-loamy over sandy or sandy-skeletal, mixed, thermic Typic Umbraquult) in Plymouth, NC; a Bojac sandy loam soil (coarse-loamy, mixed, thermic Typic Hapludult) in Painter, VA; and a Sassafras sandy loam soil (fine-loamy, silicaceous, mesic Typic Hapludult) and an Aura loam (fine-loamy, mixed mesic Typic Hapludult) in Bridgeton, NJ, in 2001 and 2002, respectively. Soil pH, native soil Ca, and planting and harvest dates varied among years and locations (Table 1). Temperatures recorded during the growing season were used to compute accumulated heat units based on the model developed by Lee et al. (1992), with 10°C as the base unit and penalties calculated when minimum or maximum temperature exceeded 21 or 25°C, respectively. The accumulated heat units were plotted to compare temperature stress among environments (Fig. 1). Tubers from each plot were mechanically harvested, sized into groups (<48, 48–64, 64–83 and >83 mm in diam.), weighed by group, and washed. Specific gravity was determined on tubers (64–83 mm) by the weight-in-air, weight-in-water method (Murphy and Goven, 1959). Tissue samples were obtained from each of 10 clean tubers (64–83 mm) from each plot using a No. 9 cork borer to obtain a longitudinal section. Tissue external to the pith was removed with a sharp stainless steel knife; tissue cores were sliced and dried at 60°C for tissue analyses. Since symptoms of IHN occur in the tuber pith tissue, the focus of this study was the mineral concentrations in the pith tissue. Pith tissue samples from all locations were shipped to a commercial laboratory (A & L Labs, Richmond, VA) to be ground and analyzed for P, K, Mg, Ca, S, Na, Zn, Mn, Cu, and Fe as a single batch each year. Tuber tissue was prepared for analyses by microwave assist open nitric/hydrochloric acid digestion using

Table 1. Soil pH, native soil Ca concentration, and planting and harvest dates for 18 potato clones evaluated in the soil-applied Ca study conducted in Bridgeton, NJ, Painter, VA, and Plymouth, NC, in 2001 and 2002.

Location	Year	Soil pH	Native soil Ca	Planting date	Harvest date	Days to harvest
			mg kg^{-1}			
Plymouth, NC	2001	5.9	918	14 March	17 July	125
Painter, VA	2001	6.8	419	9 April	16 July	98
Bridgeton, NJ	2001	6.5	961	20 April	20 August	122
Plymouth, NC	2002	5.5	–	20 March	27 July	129
Painter, VA	2002	6.4	522	25 March	22 July	119
Bridgeton, NJ	2002	6.3	747	17 April	19 August	124

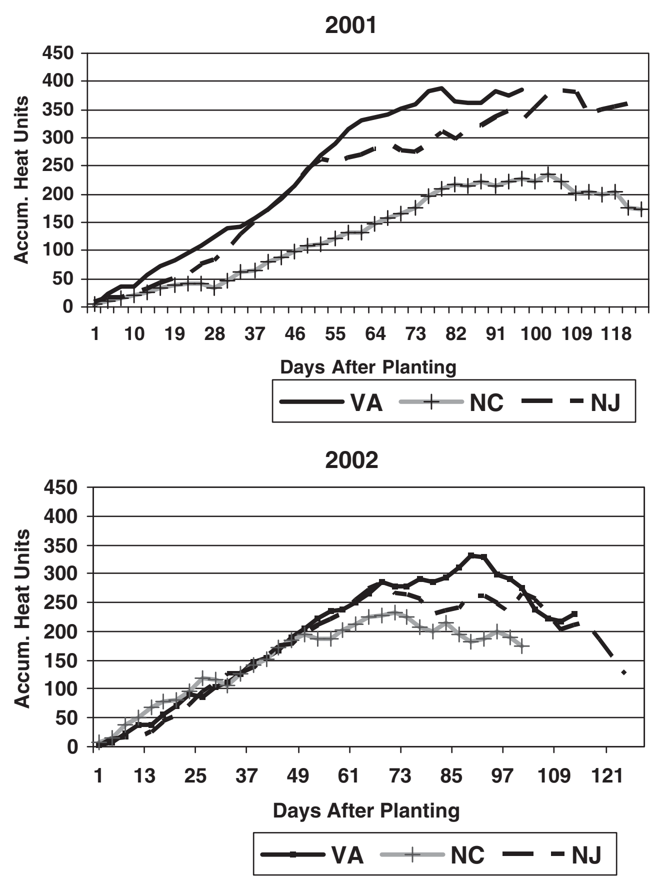

Fig. 1. Accumulated heat units according to the model of Lee et al. (1992) during the growing season for each location–year.

closed vessel microwave digestion (CEM Mars 5) then determined by inductively coupled plasma spectrometry (Mills and Jones, 1996). All tubers within each plot exceeding 64 mm in diameter were counted, quartered longitudinally (including those sampled for tissue analyses), and evaluated for IHN using a 9 (no necrosis) to 1 (severe IHN) rating scale (Sterrett et al., 1991a). For those plots with <20 tubers exceeding 64 mm in diameter, sufficient tubers from the 48- to 64-mm category were cut to total 20 tubers. Incidence of IHN (percentage of tubers expressing symptoms) and severity (mean IHN rating) were determined for each plot.

Statistical Analysis

Yield, SG, incidence, and severity of IHN, and pith tissue concentration of P, K, Mg, Ca, S, Na, Zn, Mn, Cu, and Fe were analyzed using the general linear models procedure in SAS (SAS, 1999) by location–year. Contrasts between IHN-susceptible and IHN-resistant clones were computed for all variables. Correlation coefficients between incidence of IHN and the 10 nutrients as well as among the 10 nutrients by location–years were calculated.

Incidence of IHN from each location–year was fit with a CART (Breiman et al., 1984) model using S-Plus software (S-plus, 2001). The 10 nutrients served as potential regressors, to identify subsets of nutrients and ranges of their values that are able to predict incidence of IHN. Tree models are more robust and general than stepwise regression models because they iterate exhaustively over all possible partitions of the data points to search for subsets of the data and independent variables that best predict the dependent variable. This approach is a much more specific approach than just looking for interactions among independent variables. Complex interactions among nutrients at the cellular level can be more thoroughly investigated using CART analyses since tissue concentrations of these nutrients are not independent.

RESULTS AND DISCUSSION

Fourteen variables were analyzed in this research: yield, SG, incidence and severity of IHN, and tuber concentrations of P, K, Mg, Ca, S, Na, Zn, Mn, Cu, and

Table 2. Analysis of variance on yield, specific gravity, incidence, and severity of internal heat necrosis (IHN) for 18 4×–2× clones grown in Plymouth, NC, Painter, VA, and Bridgeton, NJ, in 2001 and 2002.

Source	d.f.	Yield†	Specific gravity	PIHN‡	IHN rate§
			2001		
Rep	2	ns,¶ ns, ns	**, ns, *	**, ns, ns	**, ns, ns
Clones	17	**, **, **	**, **, **	**, **, **	**, **, **
R vs. S#	1	**, **, ns	*, **, ns	**, **, **	**, **, **
Ca	1	ns, ns, ns	ns, ns, ns	*, ns, **	**, ns, **
Clone × Ca	17	ns, ns, ns	ns, ns, ns	ns, ns, **	ns, ns, ns
			2002		
Rep	2	ns, ns, ns	**, ns, *	*, ns, ns	**, ns, ns
Clones	17	**, **, ns	**, **, **	**, **, **	**, **, **
R vs. S	1	**, **, ns	**, ns, **	**, **, **	**, **, **
Ca	1	ns, ns, ns	ns, ns, ns	ns, ns, ns	ns, ns, ns
Clone × Ca	17	ns, ns, ns	ns, ns, ns	*, ns, ns	ns, ns, ns

* Significant at the 0.05 level of probability.
** Significant at the 0.01 level of probability.
† Locations = North Carolina, Virginia, New Jersey, respectively.
‡ Percentage of tubers with symptoms of IHN, analyzed using arsine (square root) transformation.
§ Mean rating IHN for all tubers > 64 mm in diameter.
¶ ns, not significant.
# Clones resistant to IHN (R) or susceptible (S).

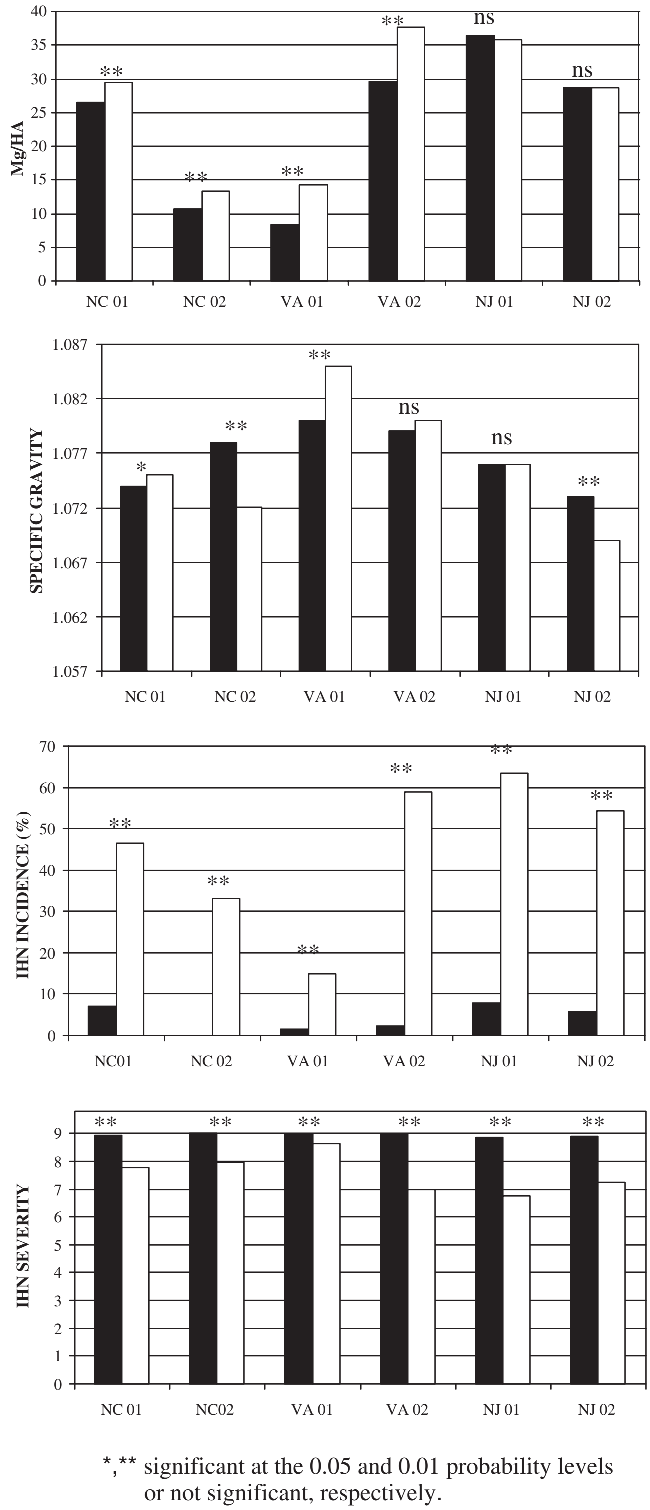

Fig. 2. Comparisons of yield, specific gravity, and incidence and severity of IHN between previously identified IHN-resistant (black bars) and IHN-susceptible (white bars) clones for each location–year. Tests of significant differences between IHN-resistant and IHN-susceptible clones within each location–year indicated above bars. *,, and ns, significant at the 0.05 and 0.01 probability levels or not significant, respectively.**

Fe. There was significant heterogeneity ($32.77 < \chi^2 < 356.14$) among the error variances for all of the variables; therefore, all data were analyzed by location–year for consistency.

There were significant differences among the clones for yield in five of the six location–years of this study and in all six location–years for SG (Table 2). The IHN-resistant clones were significantly lower yielding than IHN-susceptible clones in North Carolina and Virginia, but similar in New Jersey (Fig. 2). In 2001, Virginia accumulated heat units more rapidly than North Carolina and New Jersey during tuber bulking, which would indicate more stressful temperatures (Fig. 1). In 2002, North Carolina accumulated heat units more slowly than either Virginia or New Jersey, particularly during tuber bulking. However, *Tomato spotted wilt virus* was much more prevalent in North Carolina in 2002 and the growing season was drier. These two factors contributed to the lower yields in North Carolina in 2002. Yield was not affected by addition of Ca in this study, regardless of location–year. A similar lack of yield response to additional Ca application has been reported by others (Clough, 1994; Kleinhenz et al., 1999; Silva et al., 1991).

The relationships between SG and IHN were inconsistent among location–years, indicating a very complex biological-environment system. The IHN-resistant clones were lower than IHN-susceptible clones in SG in 2001 in North Carolina and Virginia; higher in SG in 2002 in North Carolina and New Jersey; and similar in SG in 2001 in New Jersey and in 2002 in Virginia (Fig. 2). Genotype × environment interactions can be substantial for SG (Haynes et al., 1989; Haynes, 2001; Murphy and Goven, 1959). Applied Ca had no effect on SG (Table 2). This agrees with the results obtained by Locascio et al. (1992), who also found that rate of Ca application had no effect on tuber SG.

There were significant differences among the clones for both incidence and severity of IHN in all location–years (Table 2). The clones previously identified as resistant by Sterrett et al. (2003) were consistently lower in incidence and severity (higher numbers reflect less intense IHN) than the susceptible clones (Fig. 2). Mean incidence of IHN in the resistant clones ranged from 0 to 7.9%, whereas mean incidence of IHN in the susceptible clones ranged from 14.96 to 63.54%. The IHN was also less severe in the resistant clones. Mean IHN severity ranged from 8.86 to 9.00 in the resistant clones and from 6.77 to 8.62 in the susceptible clones.

The clone × Ca interaction was significant in two of the six location–years (North Carolina 2002 and New Jersey 2001) for incidence of IHN, but not for severity of IHN (Table 2). The incidence of IHN increased in two and decreased in one IHN-susceptible clones with soil-applied Ca in North Carolina 2002 (data not shown). In New Jersey 2001, incidence of IHN decreased with soil-applied Ca in three (2 IHN-susceptible and 1 IHN-resistant) of the 18 clones tested. Linear correlations (r) between tuber Ca concentration and incidence or severity of IHN were weak, ranging from −0.25 to 0.21 and −0.19 to 0.22 in 2001 and 2002, respectively, and were significant in only two of the location–years (North Carolina 2001, New Jersey 2001). Given the large number of clones examined in this study, it is apparent that the expression of IHN cannot be consistently maintained below current USDA grade A standards of 5% tuber defects (by weight) with addition of soil-applied $CaSO_4$ in the mid-Atlantic states. Silva et al. (1991) and Davies (1998) also concluded that application of $CaSO_4$ is inconsistent in reducing Ca-related disorders.

Significant differences among clones were found in five location–years for tuber concentrations of P, K, Mg, S, and Mn; in four for tuber Ca and Zn; three for tuber Fe; one for tuber Cu; and none for Na (Table 3). However, tuber concentrations were significantly higher for IHN-resistant than IHN-susceptible clones for Mg, S, Mn, Ca, Cu, and Fe in six, five, five, four, one and one location–years, respectively, but lower for P and K in three and one location–years, respectively (Fig. 3). Tuber Zn and Na were similar in IHN-resistant and IHN-susceptible clones.

Early literature suggested a nutrient imbalance as the cause of IBS, although more recent research has focused on inadequate Ca supply or a localized Ca deficiency as the primary cause (Hiller et al., 1985). Locascio et al.

Table 3. Analysis of variance on tissue analyses for 18 4×–2× clones grown in Plymouth, NC, Painter, VA, and Bridgeton, NJ, in 2001 and 2002.

Source	P	K	Mg	Ca	S	Na	Zn	Mn	Cu	Fe
	%					$\mu g \cdot g^{-1}$				
					2001					
Rep	*, ns, ns†‡	**, *, ns	ns, ns, ns	*, **, ns	ns, ns, ns	**, **, **	*, ns, ns	ns, ns, **	**, ns, ns	ns, ns, **
Clones	**, **, ns	**, **, ns	**, **, ns	**, ns, *	**, *, ns	ns, ns, ns	**, ns, ns	**, *, ns	**, ns, ns	*, ns, ns
R vs. S	**, ns, ns	ns, ns, ns	**, **, *	*, ns, *	**, **, ns	ns, ns, ns	ns, ns, ns	**, **, ns	*, ns, ns	ns, ns, ns
Ca	*, ns, ns	ns, ns, ns	ns, ns, ns	ns, **, ns	ns, ns, ns	*, ns, ns	ns, ns, ns	*, ns, ns	ns, ns, ns	ns, *, ns
Clone × Ca	ns, ns, ns	ns, ns, ns	ns, ns, ns	ns, ns, ns	ns, ns, ns	ns, ns, ns	ns, ns, ns	ns, ns, ns	**, ns, ns	ns, ns, ns
					2002					
Rep	**, **, ns	**, *, ns	**, ns, **	**, ns, **	**, ns, ns	**, ns, **	ns, ns, ns	*, ns, **	*, –, ns	ns, ns, **
Clones	**, **, **	**, *, *	**, **, **	ns, *, **	**, **, **	ns, ns, ns	**, **, **	**, *, **	ns, –, ns	**, ns, *
R vs. S	**, **, ns	ns, **, ns	**, **, **	ns, **, **	*, **, **	ns, ns, ns	ns, ns, ns	**, **, **	ns, –, ns	ns, *, ns
Ca	ns, ns, ns	ns, ns, ns	ns, ns, ns	*, **, **	ns, ns, ns	ns, **, ns	ns, ns, ns	ns, *, ns	ns, –, ns	ns, ns, ns
Clone × Ca	ns, *, ns	ns, *, ns	ns, **, ns	ns, *, ns	ns, **, ns	ns, **, ns	ns, ns, ns	ns, ns, ns	ns, –, ns	ns, ns, ns

* Significant at the 0.05 level of probability.
** Significant at the 0.01 level of probability.
† Locations = North Carolina, Virginia, New Jersey, respectively.
‡ ns, not significant.

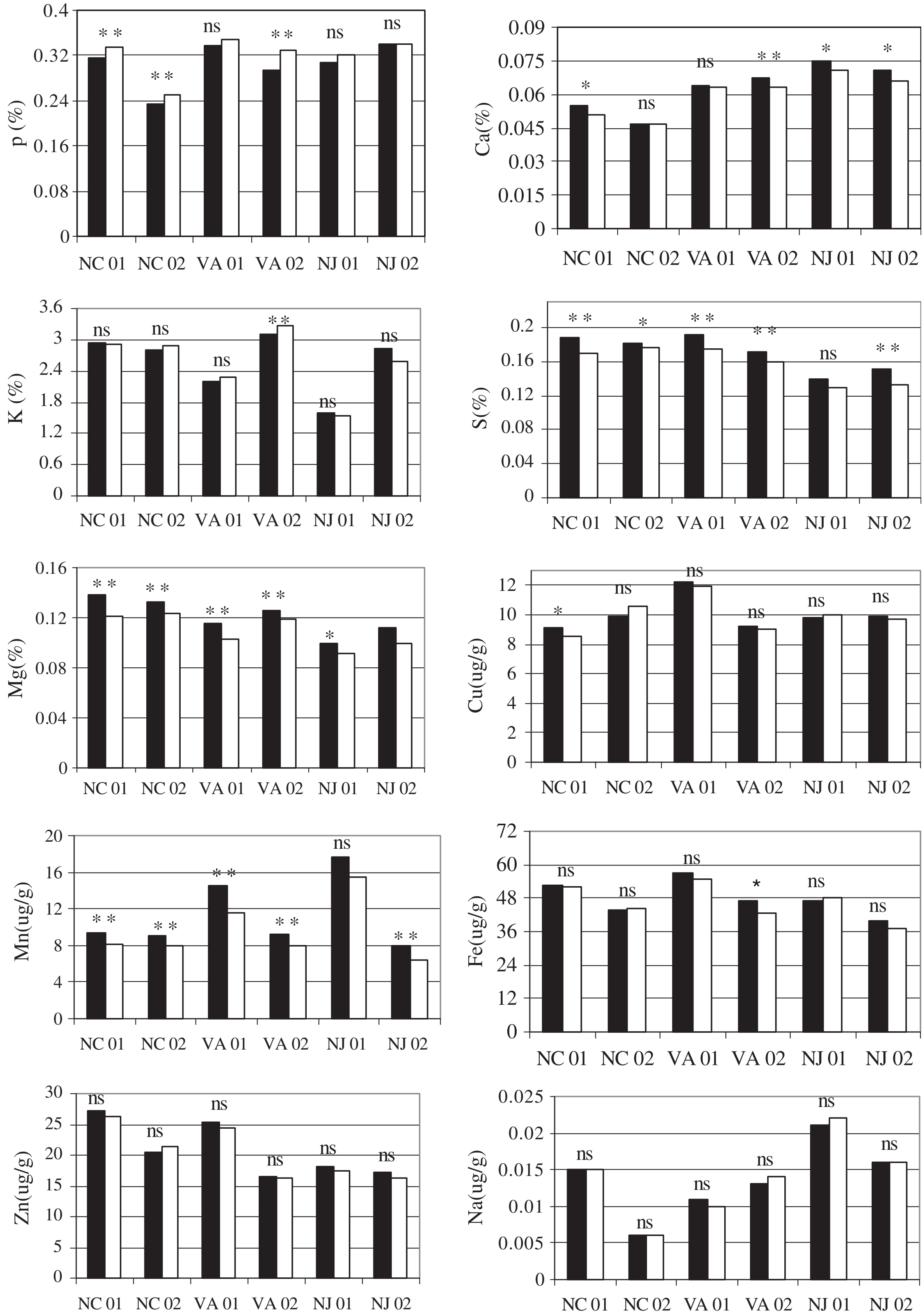

Fig. 3. Comparisons of pith tissue concentrations between IHN-resistant (black bars) and IHN-susceptible (white bars) clones for each location–year. Tests of significant differences between IHN-resistant and IHN-susceptible clones within each location–year indicated above bars. *,, and ns, significant at the 0.05 and 0.01 probability levels or not significant, respectively.**

Table 4. Correlation coefficients among the various nutrients for 18 4×–2× clones grown in Plymouth, NC, Painter, VA, and Bridgeton, NJ, in 2001 (above) and 2002 (below).

	PIHN†	P	K	Mg	Ca	S	Na	Zn	Mn	Cu	Fe
P	**, ns,‡ ns	–									
	*, **, ns										
K	ns, ns, ns	**, **, **	–								
	*, **, ns	**, **, **									
Mg	¶, §, ns	**, **, **	**, **, **	–							
	ns, ¶, §	**, **, **	**, **, **								
Ca	ns, ns, ns	ns, *, **	**, ns, **	**, **, **	–						
	*, ¶, ns	**, ns, **	**, *, **	ns, **, **							
S	¶, §, ns	*, **, **	**, **, **	**, **, **	ns, ns, *	–					
	ns, **, **	ns, ns, **	**, ns, **	**, ns, **	**, **, **						
Na	ns, ns, ns	ns, ns, *	ns, ns, ns	ns, ns, ns	ns, ns, ns	ns, ns, *	–				
	ns, ns, ns	ns, **, **	ns, **, **	ns, ns, **	ns, **, **	ns, ns, **					
Zn	ns, ns, ns	**, **, **	**, *, **	**, **, **	ns, ns, **	**, **, **	ns, ns, *	–			
	ns, ns, ns	**, **, **	**, **, **	**, *, **	ns, ns, **	**, **, **	ns, ns, **				
Mn	§, ¶, ns	ns, *, ns	ns, ns, ns	**, **, ns	ns, **, ns	**, **, ns	ns, ns, ns	ns, **, ns	–		
	¶, ¶, ¶	ns, ns, *	**, ns, **	**, **, **	ns, **, **	**, **, **	ns, ns, **	ns, ns, **			
Cu	ns, ns, ns	**, **, **	*, **, **	**, **, **	ns, ns, **	*, **, **	ns, §, ns	**, **, **	ns, **, ns	–	
	ns, ns, ns	**, **, *	**, **, **	**, **, **	**, **, **	**, *, **	ns, **, *	*, ns, **	ns, ns, **		
Fe	ns, ns, ns	ns, ns, ns	**, ns, ns	**, *, ns	ns, *, ns	*, *, ns	§, ns, ¶	**, **, ns	**, **, *	**, *, ns	–
	ns, ¶, ns	**, ns, **	**, ns, **	**, **, **	ns, **, **	**, *, **	ns, ns, **	*, **, **	**, **, **	ns, *, **	

* Positive correlations significant at $P = 0.05$.
** Positive correlations significant $P = 0.01$.
† PIHN, percentage of tubers with symptoms of IHN.
‡ ns, not significant.
§ Negative correlation significant at $P = 0.05$.
¶ Negative correlation significant at $P = 0.01$.

(1992) found cultivar differences in tuber K concentration, but reported increased tuber K with additional Ca in only 1 of 3 yr. We also found cultivar differences in tuber K concentration, but additional Ca did not increase K at any of the six location–years. Clough (1994) reported elevated tuber Ca with preplant applied Ca in 'Frontier', but not Russet Burbank. The IBS was reduced from 16.7 to 13.8% in that study, with application of 270 Mg ha^{-1} $CaS0_4$. However, tuber Ca in our trial averaged 185% of the tuber Ca reported for cultivars grown in the Clough study, and the percentage of tubers with IHN in susceptible clones exceeded 33% in five of the six location–years. Clough (1994) reported an increase in tuber S and Mn with increased preplant soil-applied Ca by 8 and 4%, respectively, while added Ca increased S and Mn by 2 and 4%, respectively, in our study. However, S and Mn found in tuber tissue in our study was 81 and 71% of that reported by Clough (1994). Clough (1994) also reported that increased preplant soil-applied Ca had no effect on tuber P, Mg, Fe, Cu, or Zn.

Many of these nutrients play important roles in multiple biochemical pathways. Correlations between any two nutrients ranged from −0.22 to 0.89 within the six location–years (data not shown), suggesting a complex interrelationship among them. More than half of the correlations among the concentrations of any two tuber nutrients were significant and positive (Table 4).

The CART analyses were used to examine the complex interactions among nutrients and IHN. The CART analyses provide advantages in dealing with dependencies among variables. The first variable to be pulled out in the split is the most important in reducing the within-group variation for that location–year. Manganese explained the most variation in four of the six location–years (Virginia 2001, Virginia 2002, New Jersey 2001, New Jersey 2002) (Fig. 4). Although the absolute values of Mn differ among these four location–years, higher concentrations of Mn were consistently associated with resistance to IHN and lower concentrations of Mn were consistently associated with susceptibility to IHN. Phosphorus explained the most variation in the remaining two location–years (North Carolina 2001, North Carolina 2002). The reason for these differences among locations is unknown.

In two of the location–years (New Jersey 2001, Virginia 2002), P was the second most important splitting variable. In all four location–years, higher concentrations of P were consistently associated with susceptibility and lower concentrations of P were consistently associated with resistance to IHN. In three of the location–years, S was an important splitting variable; higher concentrations of S were consistently associated with resistance to IHN and lower concentrations of S were consistently associated with susceptibility to IHN.

Other researchers have reported on the correlations between IHN and various tuber nutrients. Our research is the first published report on the correlations that exist among the different tuber nutrients and indicates that the individual tuber nutrients are not independent of each other. This introduces an additional layer of complexity to the analysis. Unlike ANOVAs that assume independence, CART analyses makes no assumption about independence among regressor variables, thus allowing for a more comprehensive examination of them. The CART analyses, which allow for all possible combinations of nutrients, identified Mn as the most important IHN explanatory variable for New Jersey and Virginia both years and P in North Carolina both years. However, the most significant correlations involving IHN were observed with S ($r = -0.35$, $P < 0.01$), Mn ($r = -0.35$, $P < 0.01$), S ($r = -0.35$, $P < 0.001$), Mn ($r = -0.25$, $P < 0.01$), P ($r = 0.45$, $P < 0.01$), and Mn ($r = -0.34$, $P < 0.01$), in North Carolina 2001, Virginia 2001,

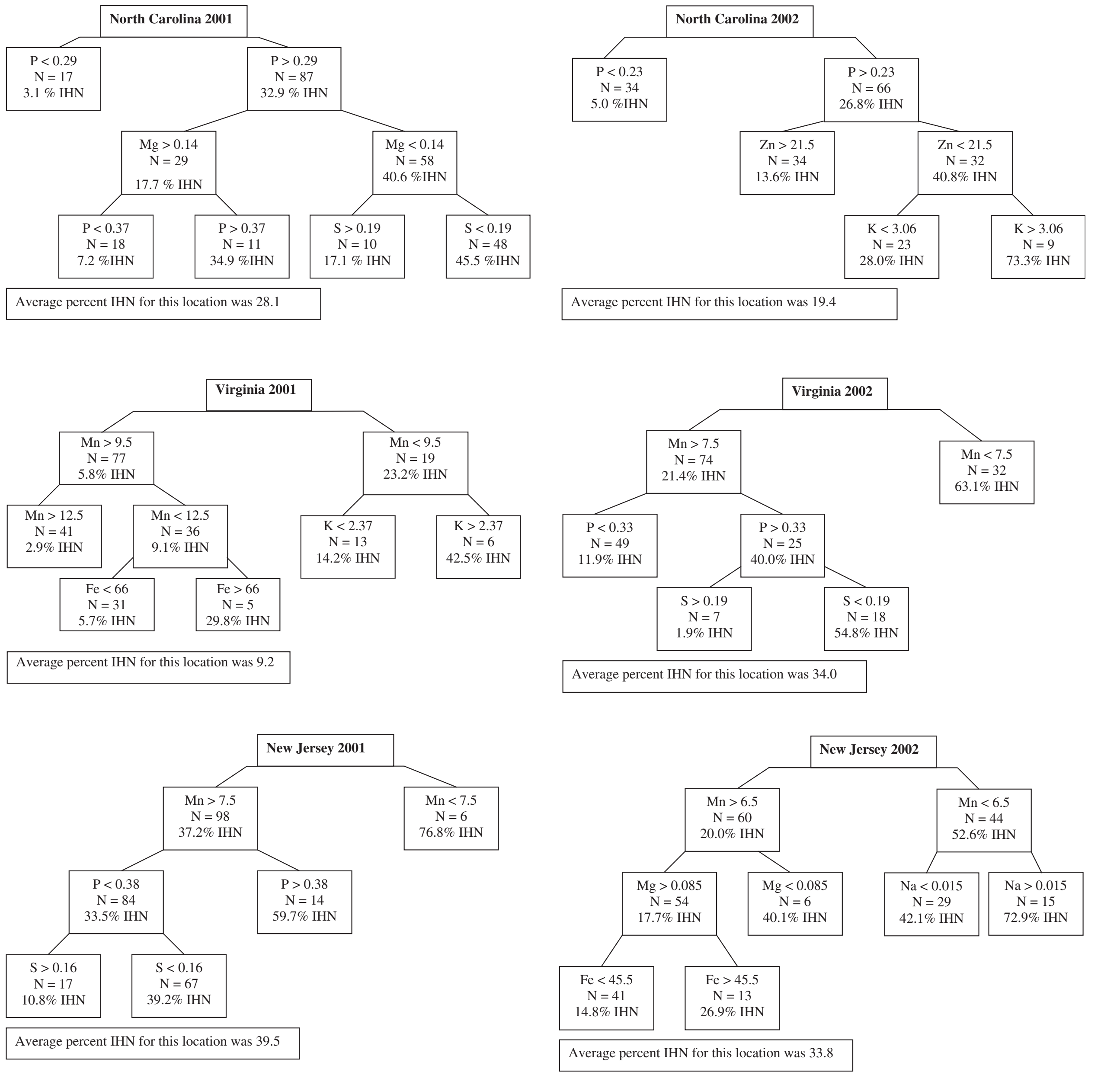

Fig. 4. Results of the CART analyses of tissue nutrient concentration on incidence of IHN for 4×–2× clones grown in Plymouth, NC, Painter, VA, and Bridgeton, NJ, in 2001 and 2002. At each branch, the tissue nutrient concentration associated with greater resistance to IHN is shown on the left-hand side of the branch and the tissue nutrient concentration associated with greater susceptibility is found on the right-hand side of the branch.

New Jersey 2001, North Carolina 2002, Virginia 2002, and New Jersey 2002, respectively. Thus, the nutrients explaining the most variation were not always the same in the CART and the correlation analyses.

Internal heat necrosis is obviously under complex biological and physiological control. The bulk of the literature to date has focused on the possible role of Ca in the expression of IHN. Our research clearly shows that Mn, P, and S explain more of the observed variation in IHN expression than Ca. In four of the six location–years of our study, no correlation was observed between Ca and either incidence or severity of IHN; in the other two location–years the correlations were opposite. Davies (1998) also found stronger correlations between IBS and Mg (−0.54) or P (−0.58) than with K (−0.38) or Ca, but poor correlations with Na, Zn, Mn, and Cu. In our study we found no correlations between incidence of IHN with Na, Cu, and Zn. However, we did find that the correlations between incidence of IHN with Mn, K, and Fe were significant in five, two, and one location–years, respectively.

More potato clones having greater genetic diversity were examined in this study than in previous studies on the relationship between IHN and tuber nutrient status. Our study examined 18 clones, whereas Kleinhenz et al. (1999) only used Atlantic, Clough (1994) studied three potato varieties, and Davies (1998) reported on eight. Both the tuber Ca concentrations of Atlantic and the incidence of IHN in our study exceeded previously published results, indicating that just increasing the tuber Ca content is not sufficient to control IHN in the mid-Atlantic states.

The results of this study suggest that higher concentrations of Mn and S, and lower concentrations of P are associated with resistance to IHN. However, there were apparently no threshold values for these concentrations. Thus, until we understand more about the underlying mechanisms governing resistance to IHN, reducing IHN by manipulating soil fertility is not feasible. Davies (1998) concluded that a plant-based rather than a soil-based solution to the problem of IHN is needed. Sterrett et al. (2003) identified high SG 4×–2× hybrids with resistance to IHN. Our research is the first reported effort to understand the differences in nutrient composition of genetic material with known resistance or susceptibility to IHN. This has brought us a step closer to a plant-based solution for IHN.

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